OAK RIDGE NATIONAL LABORATORY
MANAGED BY UT-BATTELLE FOR THE DEPARTMENT OF ENERGY

Environmental Sciences Division
P.O. Box 2008
Oak Ridge, TN 37831-6036
(865) 574-8143
Internet: jagerhi@ornl.gov Fax: (865) 576-3989

9/13/2006

Review of Final Draft 11-28-05 San Joaquin River Fall-run Chinook Salmon Population Model

This report describes an empirical model based on regression relationships derived from historical data relating salmon survival to flow for each step of the population cycle. The model does an outstanding job of fitting the historical escapement record using an empirical approach. Although I have reservations about QA/QC with spreadsheet models, such a model is accessible to those without a PhD in statistics (unlike some other models of salmon dynamics), and might lead to greater use by stakeholders. I hope the comments below are helpful.

Yetta Jager
Environmental Sciences Division

Improving Predictive Reliability. The predictive reliability of the model can be assessed by holding out data to test against for validation purposes. Alternatively, the variation associated with predictions can be assessed by removing a handful of data and refitting the model's equations using a bootstrap approach to quantify how different the model's predictions are using parameters fitted to different subsets of years.

Extrapolation is a problem for empirical models. Any flow and temperature scenarios considered should be within the range of values that occurred during the time that the empirical relationships were fitted. Likewise, if something not included in the model (like density dependence) were to become more important in future, the model would not be able to extrapolate to the new situation.

Another way of avoiding problems with extrapolation is to use a model form that is bounded to give reasonable values. For example, I would recommend something other than a power model form for survival because if extrapolation were to occur, you could get unreasonable estimates (i.e., values greater than 1 or less than zero). Logistic models are often used, or exponential models, S = a exp(-bX), so that only values between zero and one are possible for any X. To be specific, you might consider fitting the following equation using linear regression methods:

$$logit(S) = ln\left(\frac{S}{1-S}\right) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 \tag{1}$$

Where S is the survival you want to predict and X_i are predictors like temperature (Figure 16) or Vernalis flow/exports (Figure 22, 35, 40). Figure 6 already seems to use a logistic function. To back-calculate survival, use:

$$S = \frac{1}{1 + \exp\left(-\left[\beta_0 + \beta_1 X_1 + \beta_2 X_2\right]\right)} \tag{2}$$

Density dependence: I agree, in principle, that physical barriers and those sorts of engineering solutions may not be the best long-term fixes, and that focusing on DD could be used as a red herring, but I also think that this SJR model will be much more acceptable to those on all sides of the table if it allows for density dependence, which after all is a biological certainty beyond some density, particularly with the reduced amount of spawning habitat available after damming (see Achord et al. 2003). The results of our California Energy Commission-funded study of RST data in the Tuolumne River suggest that there is some density dependence because outmigrant estimates do not vary nearly as much as spawner abundances. However, there may be some disagreement between seining and RST data in this regard. A positive relationship between spawner density and fry density (Figure 28) does not contradict the density-dependence hypothesis, especially when the relationship clearly levels off beyond 12,000 females. Thus, again to avoid unreasonable predictions at high spawner densities, I don't see that it would be that much harder to fit a non-linear model to relate Mossdale smolts to spawner abundance and Vernalis flow. On page 18, a relationship to get smolt abundance at Mossdale from escapement and spring Vernalis flow is described as multi-linear. The Ricker equation below, which is what we used in the CEC analysis for daily data, could be used as an alternative. Equation 3 below shows a general or extended form of the Ricker that allows one to include other environmental predictors (e.g., Vernalis flow, Q) for calculating smolt outmigrants, Y_t for each year *t.*

$$Y_t = Esc_t \cdot e^{b_0 + b_1 Esc_t + b_2 Q_t} \tag{3}$$

Linearizing equation (3) allows this to be fit using linear regression.

$$\log_e\left(\frac{Y_t}{Esc_t}\right) = b_0 + b_1 Esc_t + b_2 Q_t \tag{4}$$

Another advantage of using this relationship is that it will not predict any smolts when there are no spawners. A Beverton-Holt relationship with covariates could also be used, and there is a generalized stock-recruitment model that permits even more flexibility and fits both types (see Jager 2000).

<u>Collinearity:</u> I would probably not choose an alternative statistical approach to deal with this issue, but the interpretation of the model should be carefully worded to acknowledge and describe collinearity between flow and other variables. My experience with Tuolumne data and that of Speed (1993) suggest that escapement covaries with flow. Presenting correlations or collinearity diagnostics, or graphically showing that there are years with high spawner density and low flow and vice versa, would address this for spawner density. After reading the SJRGA review, it appears the outlier year 1989 might be such a year, and that keeping it in the dataset might address this issue in part, but it would be good to add more years that break the correlation.

In another example, Newman and Rice (1998, 2003) mention that exposure to salinity in coastal areas covaries with flow. In their analysis, salinity is the 2nd best predictor, after release temperature (which therefore has to be controlled for in any analysis). I don't know if additional data or experiments have been done since to measure survival under conditions with low flow-low salinity or high flow-high salinity.

Newman and Rice's (1998) analysis of ocean survival data concluded that the export effect was mildly negative, which suggests overall agreement with this study in that the effect is not statistically significant. In both cases, there is a possibility raised that this is due to covariation with flow – i.e., fish released into the delta when gates are open may benefit from increased water flow (yet another predictor correlated with flow).

Collinearity does not harm prediction – predictions using the model with both covariates are best, and reduced models might be equally good. However, the parameter estimates are unstable and interpreting the relative importance of the predictors is therefore problematic. For example, in describing the importance of flow, it would be important to explain that a number of different causal mechanisms might exist by which flow is beneficial. I suppose there are good reasons to believe that flow is causally related to both escapement and salinity.

Path analysis (structural modeling) might be a good exploratory tool for examining these variables together and quantifying the various routes through which flow is influencing survival. This would be an interesting research problem in its own right.

<u>Escapement reconstruction:</u> The population replacement rate is the ratio of the size of each 3-year old cohort with the size of the cohort that produced it 3-years earlier (it is unclear if this is restricted to females as it should be). The replacement ratio is used to calibrate the model on page "Output". I am not sure of the details of how this is used -- is a solve block is used to implement the calibration or is it done using trial and error, by adjusting what input parameter(s)?

From the standpoint of population viability analysis, this ratio is comparable to lambda, and it is encouraging that it is greater than one. However, the variance on this ratio is also very important from a conservation perspective because these runs have huge variation, cyclically dipping to very low levels that, without straying, could reach zero. The approach I used in calibrating the PVA model for the Tuolumne in my dissertation (Jager 2000) was to calibrate the variation in escapement.

Second, I used "functional calibration", which compares relationships between population predictions and environmental predictors. I calibrated the relationship between spawner abundance and annual flow by adjusting smolt survivals for each hydrologic year type. One parameter in my model, the ENSO R^2 was adjusted to obtain agreement for the relationship between escapement and the ENSO-SOI index, which was basically non-existent. Correlations between escapement and the following variables: flow lagged by 2, and 3 years, commercial fishing effort, sport effort, and combined effort lagged by one year, were all compared, but not used to make adjustments. The SJRGA review recommends using harvest data in the analysis – this may be a way to use it as a check, without revising the model to incorporate it. Of course, if harvest explains a lot of residual variation, then one would want to incorporate that data into the model.

I have not fully digested the argument made in the SJRGA review about calibrating juvenile outmigrants rather than escapement, but it could only be more informative to check fit at different points in the life cycle. My concern would be the relative quality of the types of data used for comparison. Validation reflects on the data as well as the model. Using high quality, independent data that has not already been used in the model should be a priority.

I don't have any objection to calibrating against the replacement ratio, but I agree that it would be nice to evaluate other predictions as well. It is difficult for me to suggest a calibration approach without knowing as well as the authors do what parameters are likely to influence the relationships of interest, but here are some things that could be checked:

1) The most obvious type of validation is to compare observed and predicted escapement by measuring the goodness-of-fit of a regression relationship between them, where the intercept =0 means no bias and root mean square error=0 means the model is an efficient estimator of

true escapement. This test would require the model to capture variation better than the replacement ratio alone (see discussion in previous paragraph).

2) One might be interested in the correlation among escapement predicted for the three populations and that in the data. If the tributary populations are highly correlated, this is bad because they may all wink out at the same time. It is not immediately obvious to me what parameters would influence this.
3) Functional relationships not explicitly in the model might also be compared. Here, comparing the correlation between escapement and flow and between escapement and density might reveal differences in response.

Autocorrelation: Autocorrelation is an issue when testing for significance of an estimated parameter in one of the model's equations, when using the confidence intervals on parameters. It also inflates the R^2 of each individual equation. In addition, autocorrelation in an exogenous variable (e.g., flow) can inflate the estimated density dependence in some models (Williams and Leibhold 1995) -- obviously not this one, but if the changes above are implemented, this might become a concern.

It is not that difficult to take autocorrelation into account and if you are re-doing the analyses, I would go ahead and do it. In my opinion, there is no point in testing for autocorrelation using a Durbin-Watson test because it is quite certain you will find it. The approach I would recommend is using generalized least squares and modeling the covariance of residuals – this can be done very easily in SAS's Proc Mixed with about 5 statements to solve everything simultaneously. The exponential covariance model in Equation 5 represents an exponential decay in autocorrelation over time, which is what I'd recommend using. According to this model, the expected correlation between pairs of residuals is smaller when they are separated by more years. Equation 5 would be fit to the residuals of the survival regression equation to estimate λ simultaneously with the other model parameters. If you don't have access to SAS and are using another software (e.g., R or Splus), you would first get residuals using the ordinary least squares solutions for the survival models, then fit Equation 5 to residuals, construct the appropriate variance-covariance matrix (the covariance between values for year i and j in the dataset is C(i-j)), and re-solve the original regression equation for survival using generalized least squares. Technically, the estimates are biased if you solve one and then get residuals and solve the other, but that's splitting statistical hairs. I believe Proc Mixed deals with that issue in a manner that would be technically acceptable to statisticians.

$$C(\Delta t) = e^{-\lambda \Delta t} \tag{5}$$

In some cases (probably not here), including lagged predictors (flows etc.) is an alternative option for dealing with autocorrelation. Keep in mind that collinearity will increase if lagged predictors are added. Also, the SJRGA review suggests that perhaps the predictors for the survival equations for different stages should be more carefully separated (i.e., not using flow during the same period to predict survival of two successive stages), which argues against using lagged predictors. However, this might be a reasonable approach for the escapement-reconstruction equation (see Stenseth approach below).

It might be worth exploring whether a statistical approach exists for solving the combined system simultaneously. Stenseth et al. (1999) showed how three equations for survival and recruitment, which included density dependence in early life stages, reduce to an ARMA(2,1) model. Because the Stenseth et al. model includes different lags, it is possible to simultaneously estimate the proportional influence of previous cohorts by fitting the time series parameters (e.g., for lags of 2,3,4,5 years). Advantages of the Stenseth-type model are that 1) it is stochastic and gives confidence bounds on its predictions, 2) parameter estimates for all of the different equations can be obtained simultaneously-no calibration, and 3) it would avoid double counting of effects. However, it is probably not possible to do this with exogenous covariates (e.g., see Zabel et al. (2006)).

References

Achord, S., P. S. Levin, and R. W. Zabel. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? Ecology letters 6:335-342.

Jager, H. I. 2000. Predicting the viability of fish populations in a modified riverine environment. Ph.D. Dissertation. University of Tennessee, Knoxville.

Newman, K. B., and J. Rice. 2002. Modeling the survival of Chinook salmon smolts outmigrating through the lower Sacramento River system. Journal of the American Statistical Association 97:983-993.

Stenseth, N. C., O. N. Bjornstad, W. Falck, J.-M. Fromentin, J. Gjosaeter, and J. S. Gray. 1999. Dynamics of coastal cod populations: intra and intercohort density dependence and stochastic processes. Proceedings: Biological Sciences 266:1645-1654.

Williams, D.W. and A.M. Leibhold. 1995. Detection of delayed density dependence: Effects of autocorrelation in an exogenous factor. Ecology 76(3): 1005-1008.

Zabel, R. W., M.D. Scheuerell, M. M. Mcclure, and J. G. Williams. 2006. The interplay between climate variability and density dependence in the population viability of Chinook salmon. Conservation Biology 20:190-200.